ON THE CAUSE OF AUTOTOMY IN TUBULARIA.

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In the course of studies on the oxidizing and reducing powers of the various tissues and body regions of hydromedusæ the phenomenon of autotomy was observed to occur so generally and so rapidly in *Tubularia* as to invite attention to its cause. That *Tubularia* is capable of autotomy—*i. e.*, of the self-division of its body—has long been known, the process having been observed by Giard, Loeb, Driesch, Morgan, and others. Two investigators have definitely sought to determine the *cause* of the phenomenon. The conclusions of these two workers seem, however, not to be in accord. Godlewski[1] maintains that degeneration of the hydranth precedes and conditions the autotomy, so that it is a *degenerated* hydranth that is severed from the body. Morse[2]—who seems unfortunately to have overlooked Godlewski's paper—writing in this journal states that autotomy may occur without an initial degeneration in the hydranth, if one can judge of this from histological examination.

My own experience with autotomizing *Tubularia* indicates that when this process is effected very slowly and gradually, as is ordinarily the case, one can certainly sometimes find, as did Godlewski, that before the actual separation of the hydranth the latter has undergone considerable degeneration. On the other hand, I have had many autotomized hydranths to live in apparently perfect condition for three and four days. Godlewski himself notes one such hydranth which lived for two days. It is quite easy, too, to confirm Morse's statement that a rise in temperature favors the occurrence of autotomy. Nevertheless, the peculiar conditions under which I was able to observe the autotomy convinced me that neither of the above mentioned supposed causes, nor yet both combined, is the immediate or

[1] Godlewski, E., "Zur Kenntnis der Regulationsvorgänge bei *Tubularia mesembryanthemum*." *Roux's Archiv*, Vol. 18, 1904.

[2] Morse, Max, "The Autotomy of the Hydranth of *Tubularia*." BIOLOGICAL BULLETIN, Vol. 16, 1909.

adequate cause of autotomy. I therefore gave a little special attention to this subject, the results of which may be summarized here.

The particular experience which seemed to contravene the proposed causes as being the actual immediate cause was the following: If normal healthy individuals of *T. mesembryanthemum* be held by the lower stem or stolon and drawn through any one of a variety of solutions—sodium tellurite, sodium selenite, etc.—*complete autotomy may occur in less than one minute!* Clearly degeneration is not the cause of the autotomy in these cases. Other members of the colony taken from their moorings and placed in vessels supplied with fresh sea water remained for days without autotomy. When some of these were similarly drawn through pure sea water they remained intact without autotomy. It was found, moreover, that the autotomy likewise occurred even when the animal was dipped into a solution of Na_2TeO_3, $NaSeO_3$, etc., of *lower* temperature than that from which it had just been removed. Here, too, the autotomy was rapidly and decisively effected. In these cases the autotomy plainly could not have been caused by a rise in temperature; the temperature change actually being in the opposite direction. In many cases the animals were removed from water at 16° C. and drawn through a solution at 13° C.

In order to study the changes occurring in the rapidly autotomizing animals these were examined with a Zeiss binocular while being drawn through the solutions. By this means it was found: (1) that as soon as the animal touches the solution there follows a very *strong contraction* of tentacles, hypostome, peristome, etc.; (2) that the "neck" region becomes *extremely contracted* and narrow, and apparently so much weakened as to be unable longer to support the weight of the hydranth; or rather too weak to sustain the slight pull on the hydranth as it is being drawn through or lifted from the solution. The appearance here is such as to indicate that the contraction of the circular fibers of this region is of sufficient force, not only to close completely the central channel, but also to separate and crowd out many entoderm cells, and likewise to weaken their own adhesion and that of the other ectoderm cells to each other. *A vigorous con-*

traction in response to stimulation therefore seems to be the effective cause of autotomy.

It has been possible in a few instances to get a beautiful demonstration of the strength of the contraction in the "neck" region. If a tubularian be found with the gastro-vascular cavity of the hydranth well expanded and full, it can sometimes be induced—by pricking the peristome—to contract the peristome first, and thus retain the whole of the fluid of the cavity. In this condition the hydranth somewhat resembles a rubber ball; the channel to the outside being closed by the contracted peristome, and the posterior continuation with the cavity of the stem or body being interrupted by the above-mentioned contraction of the "neck" region. If now, with an appropriate blunt instrument, pressure be brought to bear upon this sphere, and the whole proceeding carried out under the binocular, one can watch everything and gauge with one's own muscles the strength of the contraction in the peristome and "neck." In the instances where I have carried out this experiment *I have never been able to force the opening of the channel in the neck region.* Some part of the hypostome wall is the first to break.

It is, too, this very strong contraction that carries the cœnosarc of the *neck region* quite away from the perisarc (see Fig. o). Probably the reason that the point of the autotomy is always so definitely localized in this "neck" region—as was first recognized by Giard[1]—is that the remainder of the slender portion of the animal is covered with a chitinous perisarc which is rather impermeable and highly protective against stimuli.

In "normal" cases—those in which the process of autotomy is extended over a period of several hours or a day or two—it is well known that a very complete histolysis of the cells in the "neck" region occurs. There is good evidence however that in these cases, too, the histolysis is preceded by a rather strong or by a prolonged contraction of this region. In very weak solutions of tellurium and selenium salts, of acids and alkalis, and even by watchful mechanical stimulation of the animal into continuously contracted state, I have been able to effect the

[1] Giard, A., "L'Autotomie dans la série animale." *Revue scientifique*, p. 629, 1887.

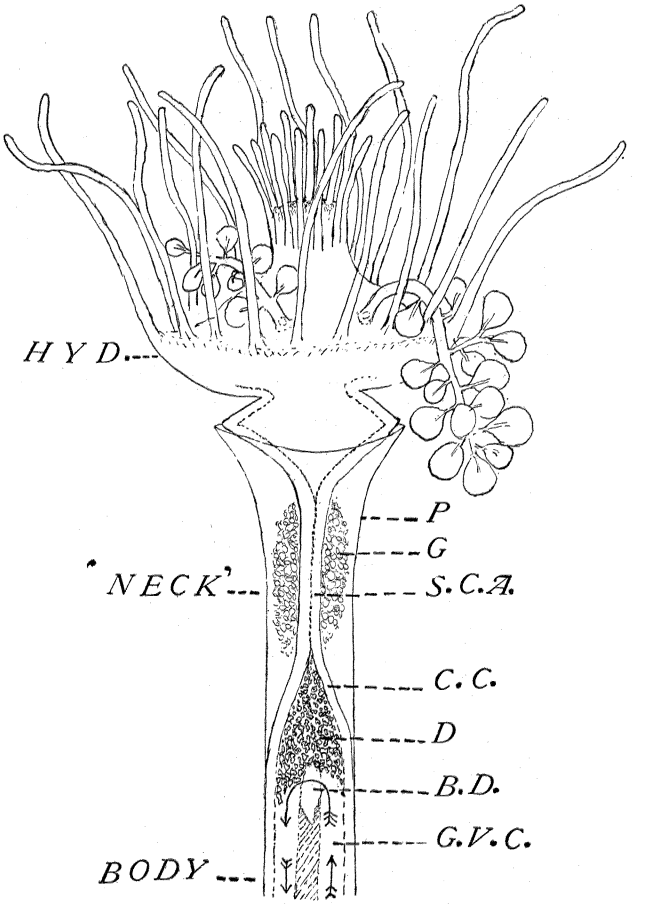
autotomy of healthy hydranths more gradually in periods extended to one to four hours, and to watch the course of the process in a single individual during this time. From these observations I may here record one or two points which seem to throw some light on the reason for the histolysis just mentioned.

I cite the case of a tubularian which was kept mechanically stimulated by touching or pricking the hydranth with a dissecting needle and in which the process of autotomy had advanced at such a rate as readily to separate at the end of four hours when lifted from the sea-water. With the beginning of contraction in this animal the circulatory current in the "neck" region was stopped; indeed the circulatory-nutritive fluids were quite expelled and excluded from approximately two millimeters of this region; the entodermic walls of the tube here being completely and tightly apposed. The closure at this point also largely stopped for a time the circulation through the stem. The fluids, however, were as before in *contact* with the walls of the gastro-vascular cavity everywhere except in the much contracted neck region. That is to say, in the contracted animal the normal nutritive fluids were in contact with all the structures with which they are normally in contact except at one point—the "neck" region; *it is always at this latter point that histolysis and autotomy later occur.*

In a little less than an hour it was found that the dissepiment which divides the gastro-vascular cavity of the stem into two channels—one for the anterior, the other for the posterior flow of the circulatory fluids—had been broken at a point a little below the contracted "neck," and that the usual *circulation* of fluids was again established within the stem. Soon however there accumulated at the point immediately below the neck a quantity of the red pigment and other débris from the circulation; thus the channel became so firmly plugged that even a relaxation of the contracted neck region could not now effect a reëstablishment of circulation in this "neck" region.

It is my opinion, furthermore, that the reëstablishment of this circulation after a few hours of contraction might be prevented or at least greatly hindered by another circumstance if for any cause the débris just mentioned should fail to collect and

act as an effective block. I refer to the accumulation of a gelatinous mass between the perisarc and cœnosarc which begins to be secreted by the cœnosarc soon after it pulls away from its contact with the perisarc. The secretion is perhaps of the nature



Representing the condition leading to autotomy in a tubularian. Such conditions are present in *Tubularia* which have been kept stimulated from one to several hours. *Hyd* = hydranth; *B.D.* = break in dissepiment; *C.C.* = cœnosarc or body wall; *D.* = debris left by circulating current; *G.* = gelatinous mass secreted by contracted cœnosarc; *G.V.C.* = gastrovascular cavity of body; *P.* = perisarc; *S.C.A.* = strongly contracted area = "neck."

of material for a new perisarc, and as noted by Godlewski it hardens on contact with water. The accumulation and hardening

of this mass would probably make a reopening of the closed channel very difficult or quite impossible.

We see then that the contraction of the contractile parts of *Tubularia* acts differentially upon its various organs. Such contraction does not rob the hydranth of its contained fluids, nor of its ability to circulate these fluids. The same is true for the stem region, except that there the actual movement of the fluids is in abeyance for a very short time. The contraction which occurs in the neck region, however, brings about far different relations between the contracting area and the nutritive medium. Here there results, not only a cessation of the circulation of fluids, but a complete loss of contact with these fluids following the complete closure of the channel; whilst finally the breaking of the dissepiment immediately below the neck region, and the subsequent plugging of the end of the connecting channel with pigment and débris, preclude the possibility that such contracted region may again regain its circulation together with the food it brings. This area then necessarily disintegrates; and the break—the autotomy—necessarily occurs at this the weakest point.

Our conclusion is that autotomy in *Tubularia* is the result of the contraction of the animal; similar but weaker contractions being common and central features in the behavior of the animal. If the contraction be either too strong, or too much prolonged, autotomy will follow. That is to say, if a very slight strain be put upon the "neck" region while its circular fibers are in a state of extreme contraction separation results at once. If the contraction be not so strong, but considerably prolonged, readjustments are effected in the circulation which prevent the ingress of food to the contracted "neck" region. Degeneration now occurs in this region and the break—the autotomy—follows at this same point. There is, then, no great mystery attached to "l'amputation spontanée"; not even a complex organic correlation to direct a watchful and sacrificial neck in severing an offending head from an unoffending body.

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